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RESPONSES OF PHOSPHATE DEPRIVATION ON PLANT GROWTH AND DEVELOPMENT

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ABSTRACT

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Phosphorus (P) is limiting for crop yield on > 30% of the world's arable land and, by some estimates, world resources of inexpensive P may be depleted by 2050. However, Pi is the least accessible macronutrient in many ecosystems and its low availability often limits plant growth. Phosphate (Pi) plays a central role as reactant and effector molecule in plant cell metabolism. Plants have evolved a diverse array of strategies to obtain adequate P under limiting conditions, including modifications to root architecture, carbon metabolism and membrane structure, exudation of low molecular weight organic acids, protons and enzymes, and enhanced expression of the numerous genes involved in low-P adaptation. Although physiological responses to Pi starvation have been increasingly studied and understood, the initial molecular events that monitor and transmit information on external and internal Pi status remain to be elucidated in plants. This review summarizes molecular and developmental Pi starvation responses of higher plants and the evidence for coordinated regulation of gene expression for significant advances in our understanding of the complex mechanisms by which plants regulate Pi-starvation responses.

Key words: Phosphorus deprivation, Pi homeostasis, plant growth, gene expression

INTRODUCTION

Phosphorus (P) is the second most limiting plant mineral after nitrogen. As world phosphorus reserves are becoming depleted, it is becoming increasingly important to understand the molecular mechanisms involved in the P-deficiency response in plants. Although plant roots readily absorb inorganic phosphate, most soil phosphate is inaccessible to plants as it is bound to many soil constituents such as iron, aluminium and calcium phosphate, forming complexes of limited availability to plants. Plants have evolved different strategies to liberate the organic P (P_0) including the secretion of organic acids, piscidic acids, and secretory acid phosphatases (S-APases) from roots. It has been suggested that S-APases secreted from roots can hydrolyze organic phosphates from the soil so liberating inorganic phosphate that can subsequently be absorbed and utilized by the plants. Acid phosphatases (APases) have also been found to play a major role in salvaging phosphate from the soil. Ultimately, increasing the availability of P_0 to plants may decrease agriculture's dependence on Pi fertilizers. Low soil phosphorus availability is a primary constraint to plant growth over much of the earth's surface, principally because phosphorus is commonly bound to soil constituents that make it unavailable to plants (Sample *et al.* 1980). In agricultural systems, low phosphorus availability has been addressed through the application of concentrated phosphorus fertilizers, but the efficiency of this

process is affected by chemical immobilization of phosphorus in soil, depletion of nonrenewable sources of phosphorus ore, and cost of fertilizer processing (Cathcart, 1980; Sanchez & Uehara, 1980; Netzer, 1987). Furthermore, intensive fertilization is a primary source of runoff pollution that threatens surface water resources in the United States and other developed nations (National Research Council, 1989; Francis *et al*. 1990). Therefore, the response of whole plants to soil phosphorus availability, including the importance of root hairs in phosphorus acquisition, is of considerable interest in agriculture and ecology. Improvement of P acquisition and use by plants is critical for economic, humanitarian and environmental reasons.

MINERAL NUTRITION IN PLANTS

Mineral nutrient deficiencies constitute the major prevalent limitation for crop productivity worldwide. Phosphorus (P), potassium (K) and nitrogen (N) (macro nutrients) are classified into essential mineral nutrients that require the greatest agricultural investment. For micronutrients, Fe is the most limiting micronutrient to agricultural yields (Kochian, 2000). High agricultural yields depend strongly on fertilizer application, with the use of the three main mineral elements - nitrogen, phosphorus, and potassium - rising steadily from 112 million metric tonnes in 1989 to 143 million metric tonnes in 1990 (Lauriente, 1995). However, most crop plants, only use less than half of the fertilizer applied (Loomis & Connor, 1992). The remaining minerals may leach into groundwater, become fixed in the soil, or contribute to air pollution.

Over the past decade, there has been considerable research investigating the molecular and physiological mechanisms of P, K and Fe acquisition and to understand more about mineral-related genes and the proteins they encode. Research has shown that mineral nutrient acquisition and homeostasis is a highly regulated and complex set of processes. The studies have demonstrated that changes in plant mineral status results in signals that ultimately are transduced and result in the alteration in expression of mineral nutrition-related genes and proteins, causing changes in mineral uptake and utilization which is beneficial to the plant (Wang *et al*. 2002).

PHOSPHORUS AND PLANT GROWTH

Phosphorus (P) is one of the most important elements for plant growth and development (Abel *et al*. 2002). Phosphorus availability is seldom adequate for optimal plant growth as it is commonly bound to many soil constituents, forming complexes of limited availability to plants (Sample, *et al*. 1980). Unlike the nitrogen cycle, the phosphorus cycle is open and tends toward depletion (Stevenson, 1986). In weathered soils, Fe and Al oxides (and in some cases recalcitrant organic matter) bind native and applied phosphorus into forms with limited availability to plants (Tarafdar & Claassen, 1988). Therefore, low phosphorus availability is a primary limitation to terrestrial plant productivity, and is often acutely limiting in the tropics and subtropics.

The Pi concentration in the soil solution is less than 10 μM (Marschner 1995) and so this makes the uptake of Pi into living cells a problem since the Pi concentration within most plant cells is 10,000-fold higher (1-10 mM, Bieleski 1973). As a result, under normal physiological conditions, plants have to acquire Pi against this huge concentration gradient (Bieleski & Ferguson, 1983). Application of phosphorus fertilizers is not an entirely satisfactory solution to this problem, because of the limited availability, high cost, and marginal effectiveness of phosphorus fertilizers for low input farmers. Further, environmental pollution results from excessive use of phosphorus fertilizers in developed countries (Sanchez, 1976). Globally, phosphate-rich ore deposits are a non-renewable mineral resource that may be depleted within the next century (Cathcart, 1980). An alternative or complementary approach is the development of crops with

higher adaptation to low phosphorus availability ('phosphorus efficiency'). Such crops would yield better in low-input agroecosystems, and would require reduced fertilizer application (and reduced environmental pollution) in higher input systems (Lynch, 1998).

Phosphorus efficiency is defined as the ability of a plant to acquire P from the soil and to incorporate or utilize it in yield production (Blair, 1993). To distinguish efficient genotypes from their genetic yield potential, Gerloff & Gabelmen (1983) proposed that germplasm differing in yields under nutrient stress could only be designated as efficient or inefficient if they have similar yields when an optimal nutrient is applied. Thus it can be hypothesized that the efficiency of genotypes is in fact their response to P-deficiency stress, and genotypes having the same yield potential may behave differently with respect to their P-deficiency stress tolerance. Genotypes can also be categorized as P responsive if they have the capacity to increase uptake or yield as the supply of the nutrient to roots is increased. For these reasons, it is important to categorize the available germplasm for their P-efficiency, as well as P-responsiveness (Gerloff, 1976).

Many studies have been documented intra-specific variations for P efficiency in various plant species and these have been proposed as a possible tool to overcome the problem of P-deficiency stress in soils (Fageria & Baligar, 1993) with the application of P fertilizers. Salinas and Sanchez (1976) divided intra-specific variations for P-efficiency in plants in two classes: the differences in relation to external critical levels of P (in the soil) and internal critical levels (in the plant). Genotypic difference in response to P-deprivation has been reported in many crops. The response of plants to low P is complex, involving P sensing, increased uptake and metabolic shifts promoting P recycling (Abel *et al*. 2002; Franco-Zorrilla *et al.* 2004). There are two groups of genes identified in response to Pi deprivation. The early genes that respond rapidly and often non-specifically to P deficiency and the 'late' genes that alter the morphology, physiology or metabolism of plants upon prolonged P deficiency. These late genes generally improve the acquisition of P or promote the efficient use of P within the plant.

Effect of Pi deprivation on root growth

Many workers have shown that root growth and development are dependent on the P status of the plants since P is relatively unavailable and immobile in many soils (Barber, 1994). The effect of P deficiency on root growth is still unclear. Several authors have observed an enhanced root growth on P deficient plants (Anuradha & Narayanan, 1991; Rychter & Randall, 1994), whilst other authors have reported a reduction of root growth under P deficiency (Kondracka & Rychter, 1997; Mollier & Pellerin, 1999). For example, studies by Narayanan & Reddy (1982) on several plant species and Anuradha & Narayanan (1991) on horsegram reported increased primary and secondary root elongation in P-deprived plants. Similar results are also reported by Rychter & Randal (1994) on root biomass of bean. Other studies by Anghonini and Barber (1980) observed an increase in root length and dry weight on 12-d-old maize plants when the duration of the P starvation increased between 1 and 6 d. Thus effects of P deficiency on root biomass and root length are still controversial.

In contrast, some workers observed a reduction in root length and biomass for a wide range of species and experimental conditions in P-deficient plants (Rosolem *et al*. 1994). Other studies by Mollier & Pellerin (1999) showed that root growth was slightly enhanced a few days after P starvation, but strongly reduced thereafter. Other researchers reported that root growth is independent of Pi deprivation (Radin & Eidenbock, 1984). For example, Hayes *et al*. (2004) using two cultivars of wheat (cvs Brookton and Krichauff) which differ in P-uptake efficiency in the field, observed no significant different in root weight when grown in solution culture in P-sufficient or P-deficient media. They also showed that there were also no significant

effects of cultivar or P treatment on measured root surface areas. Also, Khamis *et al*. (1990) using maize and Sicher & Kremer (1988) using barley reported no effect of P deprivation on root biomass. Other studies in soybean have shown that root growth was much less affected by low-P, and no significant reduction in root growth was observed until day 17 (Freeden *et al*. 1989). At day 21, low-P plants had a 24% reduction in root DW. Studies by Nielsen *et al*. (2001), using common bean, showed that although genotypes have no significant difference in carbon assimilation, low phosphorus plants utilized a 40% fraction of their daytime net carbon assimilation to root respiration while medium and high phosphorus plants allocated only about 20% of their daytime net carbon assimilation to root respiration. They also found no significant difference in P absorption per unit root weight and plant growth per unit P absorbed. Furthermore, relative to P-inefficient genotypes, P-efficient genotypes allocated a larger fraction of their biomass to root growth under low P conditions. They also showed that a lower root respiration rate in efficient genotypes enables them to maintain a greater root biomass allocation without increasing root carbon costs.

The mechanism by which P deficiency affects root growth still remains unanswered. Anuradha & Narayanan (1991) proposed that P deficiency affects root elongation through its effect on H^+ ion excretion by roots and subsequent effects on cell wall loosening. Other workers, for example Amijee *et al*. (1989), suggest a direct effect of the P inflow in roots on their density of branching. Mollier & Pellerin (1999) suggested that P deficiency mainly affects the carbon budget of the plant and has no direct effect of P deficiency on root morphogenesis. These results are in accordance with the results of many workers who observed a higher root:shoot ratio in P-deficient plants which associated with a higher proportion of carbohydrates being partitioned to the roots and a higher sugar concentration in the roots (Cakmak *et al*. 1994; Rychter & Randal, 1994;).

Effect of Pi deprivation on shoot growth

Shoot weight and Pi uptake were shown to be the most sensitive plant parameters to P deficiency (Fageria & Baligar, 1999) and reduced shoot growth is generally observed for plants during P-deprivation (Whiteaker *et al*. 1976). A study by Hammond *et al*. (2003), using Arabidopsis, showed no significant difference in shoot fresh weight of plants grown in +P or –P for at least 72 h after P was withdrawn. However, 216 h after P was withdrawn shoot FW of plants grown without P was significantly lower relative to plants grown in P-sufficient solutions. In soybean, low-P treatment reduced shoot growth significantly 7 days after treatment began (Freeden *et al*. 1989). After 21 days, plants grown in low-P had a shoot DW of less than 17% of that of high P-plants. In another study, Hayes *et al* (2004) used two cultivars of wheat that differ in P-uptake efficiency in the field and compared their performances in solution culture. In soil, with similar biomass accumulation, the cv. Brookton accumulated 32% more P than the cv. Krichauff. In solution culture at 1 µM Pi and 10 µM Pi, cv. Krichauff (the less efficient cultivar) grew better compared to cv. Brookton (Hayes *et al*. 2004). Other workers suggested that the increase in shoot growth in P-deprived plants is a direct consequence of a reduction of leaf expansion and reduced leaf initiation (Lynch *et al*. 1991) possibly by decreasing root hydraulic conductance (Radin & Eidenbrock, 1984) and by reducing cytokinin transport from root to shoot (Horgan & Wareing, 1980).

Effect of Pi deprivation on Root:Shoot Ratio

A general response to low P availability is to increase the relative biomass allocation to roots. An increase in the root-to-shoot ratio is often observed in plants in response to P derivation (Zhu & Lynch, 2004). This increase in root:shoot ratio may enhance phosphorus acquisition as well as reduce growth rates by diverting carbon production to the roots (Cakmak *et al*. 1994; Rychter & Randal, 1994;

Trull *et al*. 1997). Zhu & Lynch (2004) reported an increased root:shoot ratio of maize plants by approximately 39% in plants grown in low P media. In wheat, the R:S ratio is reportedly highly dependent on the wheat genotype (Sadhu & Bhaduri, 1984). Furthermore, under P deficiency, P-efficient wheat varieties tend to enhance their root growth (Römer *et al.* 1988). With more root length per unit above ground biomass, the wheat plants are able to access more P resources in the soil and improve P uptake.

Studies by Nielsen *et al.* (2001) using four common bean genotypes with different adaptations to low P availability in the field showed that although these common bean genotypes had similar rates of P absorption per unit root weight and plant growth per unit P absorbed, P-efficient genotypes allocated a 20% fraction of their biomass to root growth especially under low P conditions. It was also shown that efficient genotypes had lower rates of root respiration when compared with inefficient genotypes. This suggested that efficient genotypes are able to maintain greater root biomass allocation without increasing overall root carbon costs (Nielsen *et al.* 2001).

Effect of Pi deprivation on leaf area and weight of individual leaf

Reduction in leaf area is commonly observed during Pi deprivation. Phosphorus deficiency was shown to severely reduce the leaf area of several species. This is consistent with the results of other authors who have reported a rapid and severe effect of Pi deprivation on leaf growth (Mollier & Pellerin, 1999**).** For example, Radin & Eidenbock (1984) showed that Pi deprivation in cotton caused reduction in leaf expansion through interactions with water transport, while Lynch *et al.* (1991) showed that reduced leaf area development was associated mainly with reduced leaf appearance and its morphological determinants, rather than reduced elongation of individual leaves and final leaf size. Further, in soybean, Freeden *et al.* (1989) showed that total leaf area was slightly affected by low-P treatment with a decrease to 15% in plants grown in low-P treatment. This is followed by reductions of 67% in mean leaf area, and 43% in leaf emergence. In addition, foliar application did increase the final leaf area at all P levels. Other work by Mollier & Pellerin (1999) reported that Pi deprivation caused reduction in leaf area by about 20% relative to the control. By day 16, total leaf area of P deprived plants was reduced to about 80% of that of the control. These workers thus proposed that this was the consequence of a slower rate of leaf appearance and a reduced final size of individual leaves.

Effect of Pi deprivation on biomass accumulation

Phosphorus deficiency substantially reduced total biomass accumulation. This reduction in total biomass accumulation is determined by many physiological and biochemical changes in plants under P deficiency. Plants grown in high phosphorus soil produced significantly more total dry matter than those grown in the low phosphorus soil from day 24 onwards. Further Gaume *et al*. (2001) showed that P deficiency in hydroponic culture resulted in decreased dry matter production of the four maize genotypes. The decrease was especially evident in the low-P tolerant *NTS* and acid-tolerant *Sikuani.* A significant difference in biomass accumulation was observed by Hayes *et al*. (2004) using two cultivars of wheat in solution culture that differ in P-uptake efficiency in the field. In soil, with similar biomass accumulation, cv. Brookton (the P efficient cultivar) accumulated 32% more P than cv. Krichauff (the less efficient cultivar). However in solution culture, at 1 µM Pi and 10 µM Pi, cv. Krichauff grew better. Other workers have shown that the final reduction of biomass production during Pi deprivation is as a result of reduction in leaf area and reduction of net photosynthesis per unit leaf area (Qui & Israel, 1994; Rodriguez *et al.* 1998). However, several authors have shown that plant growth under P deficiency is usually reduced before the

photosynthesis rate per unit leaf area was observed (Qui & Israel, 1994).

STRATEGIES ADOPTED BY PLANTS TO WITHSTAND Pi-DEPRIVATION

Plants have different metabolic, biochemical and developmental strategies for adapting to limited Pi supply. These comprise (1) those aimed at a conservation of P, and (2) those directed toward enhanced acquisition or uptake (Horst *et al*. 2001; Vance 2001, Playsted *et al*. 2006). The former processes include decreased growth rate, increased growth per unit of P uptake, remobilization of internal Pi, modifications in carbon metabolism that bypass P-requiring steps, and alternative respiratory pathways (Uhde-Stone *et al*. 2003a; 2003b).

Developmental responses mainly involve changes in root architecture that enhance the root surface/soil volume ratio and, as a result, the ability of the plant to access soil phosphate. These changes include, for example, increases in the root-to-shoot ratio, the number of lateral roots and the number and length of root hairs (Wang *et al*. 2004; Zhu & Lynch, 2004). Furthermore, some plants have the ability to form cluster roots or to establish a symbiotic association with mycorrhizal fungi (Burleigh *et al*. 2002; Vance *et al*. 2003; Glassop *et al*. 2005). Moreover, at extremely low P supply, nonmycorrhizal Cyperaceae species can form dauciform roots (rootlets densely covered with long hairs) that comprise up to a quarter of a root biomass (Shane *et al*. 2005). It has also been shown that lateral roots prefer to proliferate in areas of high Pi content and are retarded in the low Pi areas (Shane *et al*. 2005).

Pi DEPRIVATION INDUCED CHANGES IN GENE EXPRESSION

In an effort to understand the molecular mechanisms underlying P stress, attempts have turned toward the isolation of genes regulated by P supply. This also permits insight into their functions and the pathways that lead to their expression. Although several responses of plants to P deprivation, including short term metabolic and physiological changes, may not require changes in gene expression, the majority are predicted to rely on alterations in gene expression. The most important questions to be asked with respect to P deprivation are: (1) what genes are induced or repressed during Pi deprivation? (2) what is the function of the encoded gene products?, and (3) how are these genes regulated? It is clear now that many of the biochemical, physical and morphological changes which occur in response to Pi starvation are associated with altered gene expression (Plaxton & Carswell, 1999; Raghothama, 1999).

Altered gene expression in response to phosphorus deprivation has been demonstrated in the roots of *Arabidopsis*, tomato, rice, white lupin, and white clover. These genes encode proteins involved in P metabolism, carbon metabolism, glycolysis, and lipid metabolism, as well as coding for a high affinity Pi transporter, lignin synthesis-related genes and secondary metabolites. Many of these genes have been cloned and their responsiveness has demonstrated the importance of transcriptional control in the regulation of these responses in plants. For example, a *LePS2* (a gene involved in internal remobilization of P from tomato) transcript was detected within 24 h after Pi-starvation in roots and shoots and it continued to increase with an extended duration of the Pi starvation period reaching a maximum at day 5. In cell culture, rapid induction of *LePS2* was observed within 3 h after transferring tomato cell cultures to a Pi-deficient media. This indicates a rapid response to Pi deficiency in the culture media. This result is in agreement with the data showing that APase activity was induced within 24 h of transferring tomato cells to Pi-deficient medium (Goldstein *et al*. 1988).

Pi HOMEOSTASIS AND SIGNAL TRANSDUCTION DURING Pi DEPRIVATION

In order to overcome problems with P availability, plants have evolved a series of adaptive responses to maintain Pi homeostasis. These responses include conservation and remobilization of internal P and enhanced acquisition of internal P (Raghothama, 1999; Poirier & Butcher, 2002). It has been shown that Pi homeostasis plays an important role within plant cells. This requires monitoring of the Pi concentration in cellular compartments/organelles such as the cytoplasm, vacuole, plastids and mitochondria. When a plant is Pi sufficient, about 85-95% of the total Pi is stored in the vacuole (Bieleski & Ferguson, 1983). However, in Pi-deprived plants, almost all Pi is found in the cytoplasm and chloroplasts. This represents parts of the 'metabolic pool' of Pi in the plant (Marschner, 1995). Studies in maize roots showed that under Pi deprivation, the vacuole acts as a Pi reservoir to maintain the cytoplasmic Pi pool constant and the latter does not decrease until Pi stress becomes severe (Lee *et al*. 1990).

Studies using the *Arabidopsis* mutants *pho1* and *pho2*, which are defective in Pi homeostasis, showed that Pi concentration in the leaves of *pho1* was strongly reduced while Pi concentration in the roots was similar to that of wild type plants (Poirier *et al*. 1991). This suggested that the *pho1* mutant was impaired in a protein involved in loading of Pi into the xylem in the root. In Arabidopsis, Chiou *et al*. (2006) showed that the mechanism of Pi homeostasis involves the suppression of an ubiquitin-conjugating E2 enzyme by a specific mircoRNA, namely miR399. Under Pi deprivation, the miR399 is upregulated and its target gene, E2, is downregulated. Using transgenic Arabidopsis overexpressing miR399, they showed that the accumulation of the E2 transcript is suppressed. Further they observed that transgenic plants accumulated five- to six-fold higher Pi levels in the shoots and showed Pi toxicity symptoms similar to E2 mutant. It is further shown that Pi toxicity is caused by an increase in Pi uptake, translocation and retention in the shoots. Unlike wild-type plants, remobilization of Pi in miR399 transgenic plants were impaired (Chiou, *et al*. 2006). These results prove that miRNA controls Pi homeostasis by regulating the components of the proteolysis machinery in plants.

CONCLUSION

Considering that P is an essential and often limiting nutrient for plant growth, it is surprising that many aspects of P uptake and transport in plants are not thoroughly understood. Perhaps the next important leap in our conceptual understanding in this area will come from the improvement of P acquisition and use by a plant which has immediate and direct benefit in extensive agriculture in developing countries where access to fertilizers is limited. Furthermore, because improved P acquisition and use by plants has immediate and direct benefit in extensive agriculture in developing countries where access to fertilizers is limited, funding for research at international centers should be a high priority. A final issue to raise is that the soil Pi concentration has often been ignored by plant physiologists. It is common to find experiments in which plants were grown in 1 mm Pi, which may be 100-fold higher than the Pi concentrations plants encounter in agricultural or natural ecosystems. To fully understand how plants acquire Pi from soils and regulate internal Pi concentrations, future studies on Pi uptake by plants must more closely mimic soil conditions, in which the concentration of Pi is always low and soil microflora influence both acquisition and mobilization.

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